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1 The social network structure of a dynamic group of dairy cows: from individual to group level
2 patterns

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22 ABSTRACT

23 Social relationships have been shown to significantly impact individual and group success in wild
24 animal populations, but are largely ignored in farm animal management. There are substantial gaps in
25 our knowledge of how farm animals respond to their social environment, which varies greatly
26 between farms but is commonly unstable due to regrouping. Fundamental to addressing these gaps is
27 an understanding of the social network structure resulting from the patterning of relationships between
28 individuals in a group. Here, we investigated the social structure of a group of 110 lactating dairy
29 cows during four one-month periods. Spatial proximity loggers collected data on associations between
30 cows, allowing us to construct social networks. First we demonstrate that proximity loggers can be
31 used to measure relationships between cows; proximity data was significantly positively correlated to
32 affiliative interactions but had no relationship with agonistic interactions. We measured group-level
33 patterns by testing for community structure, centralisation and repeatability of network structure over
34 time. We explored individual-level patterns by measuring social differentiation (heterogeneity of
35 social associations) and assortment of cows in the network by lactation number, breed, gregariousness
36 and milk production. There was no evidence that cows were subdivided into social communities;
37 individuals belonged to a single cluster and networks showed significant centralisation. Repeatability
38 of the social network was low, which may have consequences for animal welfare. Individuals formed
39 differentiated social relationships and there was evidence of positive assortment by traits; cows
40 associated more with conspecifics of similar lactation number in all study periods. There was also
41 positive assortment by breed, gregariousness and milk production in some study periods. There is
42 growing interest in the farming industry in the impact of social factors on production and welfare; this
43 study takes an important step towards understanding social dynamics.

44

45 **Keywords:** Social networks – Group structure – Proximity loggers - Dairy cows – Assortment –
46 Welfare

47

48 INTRODUCTION

49

50 In the UK dairy industry there is considerable diversity in the way animals are grouped and managed;
51 group sizes and stocking density vary greatly across farms, and regrouping cows during lactation
52 (based on yield or parity etc.) is common practice. Numerous studies have demonstrated the negative
53 welfare and productivity consequences of regrouping, including reductions in milk yield, feed intake,
54 rumination and lying times, and increased aggression between cows (Hasegawa, Nishiwaki,
55 Sugawara, & Ito, 1997; Hultgren & Svensson, 2009; Raussi et al., 2005; von Keyserlingk, Olenick, &
56 Weary, 2008). Agonistic interactions such as threat gestures, chasing and head butting, often result in
57 displacements from resources, but can escalate to prolonged (and more injurious) fights. The latter
58 are less frequent in stable social groups (Reinhardt & Reinhardt, 1981) as a well-established
59 dominance hierarchy shortens agonistic events or prevents them through active avoidance, profiting
60 both dominant and subordinate animals (Gurney & Nisbet, 1979).

61 Within a stable social group many cows form preferential social bonds, which may differ
62 between activities such as feeding or social grooming (Gygax, Neisen, & Wechsler, 2010; Reinhardt
63 & Reinhardt, 1981). Preferred social partners can influence status in the social hierarchy (Reinhardt &
64 Reinhardt, 1981) and their presence or absence can affect stress responses (McLennan, 2012). Social
65 grooming can be used as an indicator of affiliative relationships among social animals (Boissy et al.,
66 2007; Wasilewski, 2003), with the strength of social bonds often reflected by the degree of grooming
67 between individuals. Social grooming is believed to have a calming effect on cows (S. Sato, Sako, &
68 Maeda, 1991; S. Sato & Tarumizu, 1993), and plays a role in reducing social tension and maintaining
69 social stability (Benham, 1984; Boissy et al., 2007; Shusuke Sato, Tarumizu, & Hatae, 1993).
70 Interestingly, social grooming has been linked to production; it has been positively correlated with
71 both milk yield and weight gain in past studies (Arave & Albright, 1981; S. Sato et al., 1991). The
72 social preferences of cattle are also reflected in their spatial proximity to others in the group
73 (Bouissou, Boissy, Le Neindre, & Veissier, 2001), thus the ability to maintain suitable inter-individual

74 space is important to cows (Bøe & Færevik, 2003). In fact, Miller and Wood-Gush (1991) suggest the
75 lower levels of agonistic behaviour exhibited by cows at pasture (compared to indoor-housed cows) is
76 due to a greater opportunity to avoid others.

77 As the dairy industry becomes more aware of the impact the social environment can have on
78 welfare and production, there is growing demand for information on optimal size, stocking density
79 and composition of dairy cow management groups. In order to begin answering questions on the most
80 effective social conditions for cattle, we first need to accurately measure and understand their social
81 dynamics and group structure. Social network analysis (SNA) has been developed to quantitatively
82 measure and analyse the structure of groups and patterns caused by dyadic social interactions (Croft,
83 James & Krause, 2008). A network is made up of nodes (individuals; cows in this case) and edges
84 (interactions; association time in this case). We can calculate statistics for individuals in the network
85 such as ‘degree’ (number of edges for a given node) and ‘betweenness centrality’ (number of shortest
86 paths between pairs of individuals that pass through a particular individual) (Krause, Lusseau, &
87 James, 2009). These methods allow us to study non-random patterns of association, and detect
88 differences in group structure that may be linked to individual attributes (Croft et al., 2008). SNA is
89 becoming more popular in the field of animal behaviour, however its potential for improving animal
90 welfare in captive populations is currently underappreciated, with only a handful of empirical studies
91 to date (e.g. rhesus macaques; McCowan, Anderson, Heagarty, and Cameron (2008), Atlantic salmon;
92 Cañon Jones et al. (2010), pigtailed macaques; Flack, Girvan, De Waal, and Krakauer (2006),
93 domestic chickens (Abeyesinghe, Drewe, Asher, Wathes, & Collins, 2013)). Though few, these
94 examples establish very promising applications of SNA in animal management and have been centred
95 on reducing aggression and improving social cohesion. They suggest an important future role for SNA
96 in animal welfare science (Koene & Ipema, 2014).

97 In this study, we quantified the social network structure of a group of lactating dairy cows,
98 collecting association data using spatial proximity loggers. We corroborated this method by
99 determining how well associations measured by the proximity loggers matched agonistic and
100 affiliative interactions recorded during behavioural observations. We predicted that data collected by

101 the proximity loggers would closely resemble affiliative interactions, but would not resemble
102 agonistic interactions. Group-level structure was measured by testing for communities, betweenness
103 centralisation, and assessing network stability over time. We investigated individual-level structure by
104 determining whether individuals formed socially differentiated relationships, and by assessing the
105 extent to which cows were assorted by attributes (lactation number, breed, gregariousness and milk
106 production).

107

108 METHODS

109 *Animals and housing*

110 The study was carried out on a commercial dairy farm in Devon, UK from November 2012 to June
111 2013, in the form of 4 one-month data collection periods (see table 1). The farm comprises a 1045m²
112 (approx.) barn with straw yard housing and a voluntary milking system operating two Delaval robotic
113 milking units. A total mixed ration was fed twice daily (approx. 9am and 5pm) at a feed barrier and
114 additional concentrate feed was provided during milking and at an out-of-parlour feeder. At any given
115 time the milking group contained between 106 and 113 lactating cows. Due to year-round calving,
116 group structure was dynamic with cows entering and leaving depending on calving and drying off
117 dates, in addition to sale or culling. The total number of unique cows present throughout the study was
118 134. The group was of mixed breed though the majority were Holstein–Friesian (see table 1 for more
119 details on cows included in the study). A charolais bull was added to the milking group on 07-05-13,
120 and was therefore present within the fourth period of data collection only.

121 Although managed and housed as a single milking group, pasture access was regulated (via
122 electronic collars) based on each cow's stage of lactation. Cows were restricted to the barn in the early
123 part of their lactation, however after both testing positive for pregnancy and when milk yield dropped
124 below a threshold of approximately 26 litres, they were also given free access to pasture. All cows
125 were thus able to mix when inside the barn, but there were physical constraints to group synchrony
126 when any cows with access chose to enter the pasture. As this affected some cows' ability to associate,
127 we incorporated this management factor into all null models used in our analyses.

128 Individual attribute data (lactation number, breed, last calving date and milk yield) were
129 downloaded from the on-farm computer system (Delprom). The number of days in milk (DIM) for each
130 cow was determined as the number of days from the last calving date to the first day of each data
131 collection period. We summed the daily milk yield over each data collection period for each
132 individual.

133 *Spatial proximity loggers*

134 The proximity loggers used in this study were manufactured by Sirtrack Ltd (New Zealand), and are
135 supplied as ready-made collars to attach around cows' necks (model E2C181C). These devices
136 broadcast unique identification codes over an ultra-high frequency (UHF) channel while
137 simultaneously searching for the ID codes of others within a pre-set distance range. Each logger is
138 able to detect up to eight others simultaneously; recording its ID, the date, start and end time of the
139 contact and its duration. The detection distance may be altered by users, by adjusting the power
140 setting of a UHF coefficient range (0–62). The duration that any two loggers need be separated for an
141 encounter to terminate (“separation time”) can also be adjusted prior to deployment. Here, proximity
142 loggers were set to a UHF value of 47 (which logged contacts at 1.5–2m in pilot tests using collared
143 horses) with a separation time of 120s. Due to memory fill rate we deployed and removed loggers on
144 four occasions so that data could be downloaded, hence we divided our analyses into four data
145 collection periods (hereafter referred to as deployments 1–4).

146 *Proximity logger data handling*

147 Data collected by proximity loggers consisted of dyadic associations over time. We summed the
148 duration of all associations between dyads within each deployment period and these values were used
149 to construct social networks. As advised in previous studies (Drewe et al., 2012; Prange, Jordan,
150 Hunter, & Gehrt, 2006) we removed all 1-second contact records from the database prior to analysis,
151 as these are considered unreliable, occurring sporadically when individuals are at the edge of the
152 detection range (Drewe et al., 2012; Prange et al., 2006). Only loggers that functioned fully (both
153 sending and receiving signals) for the whole deployment period were included in analysis. We

154 therefore omitted data from broken loggers, and from cows that entered or left the milking group (or
155 whose loggers fell off) mid-way through a deployment (see table 1 for the number of individuals
156 included in analyses for each deployment). As a result of this, and the turnover of cows throughout the
157 study period, group membership differed across the deployments. It is important to note that as battery
158 power decreases over time (which is expected to affect logger function - see Drewe et al. (2012)), we
159 analysed each deployment separately and did not make any quantitative comparisons between the
160 deployments.

161 *Logging bias correction*

162 Previous work has shown that spatial proximity loggers can exhibit a sampling bias due to inter-
163 logger variation in performance (Boyland, James, Mlynski, Madden, & Croft, 2013). This is made
164 evident by association matrices with highly variable dyadic reciprocity; contact durations between
165 dyads should be mirrored if loggers are functioning uniformly. We therefore adjusted data using
166 correction methods from Boyland et al. (2013). This involved scaling all contact durations in an
167 association matrix relative to the performance of each given logger when compared with the most
168 under-recorded logger. This was achieved by calculating the percentage difference in contact
169 durations (e.g. the percentage difference between the total time logger A recorded contact with logger
170 B, and the total time logger B recorded logger A) between all dyads, then identifying the logger that
171 was most under-recorded, overall. The total contact duration (all contacts summed over the
172 deployment period) for each dyad was then reduced according to their logging bias with the most
173 under-recorded logger. For example, if logger A had a logging bias of 10% when compared to the
174 most under-recorded logger, the duration that logger A recorded contact with all other loggers would
175 be reduced by 10%. We thus standardised associations between loggers relative to each other. We used
176 Spearman's correlations to calculate the reciprocity between each side of the matrix (about the
177 diagonal) both before and after application of this correction to assess its efficacy. This resulted in
178 Spearman's r increasing from 0.72 to 0.93, 0.59 to 0.91, 0.56 to 0.72, and 0.67 to 0.92 ($p < 2.2e-16$ in
179 all cases) for deployments 1-4 respectively. We symmetrised the corrected matrix by averaging values
180 within each dyad (as proximity cannot be directed), before creating social networks.

181 *Measuring the relationship between proximity data and social interactions*

182 In order to quantify how proximity logger data relates to social relationships, we compared the
183 association strengths measured by the proximity loggers with measures of observed social interactions
184 between cows. We undertook 160 hours of behavioural observations in which 10 focal cows (chosen
185 at random) wearing proximity loggers were observed for 4 hours/day on 4 days (therefore a total
186 observation duration of 16 hours for each cow), during deployment 4. Focal cows varied in age (2-10
187 years old), lactation number (1-7), breed and DIM (30-112). During the behavioural observations,
188 each cow was followed for a total of 4 hours in a day, usually separated by periods of lying (during
189 which observations were paused). We recorded all agonistic and affiliative interactions (continuous
190 sampling), including the identity of individuals interacting with the focal cow. Chasing, head butting,
191 head shaking and threat gestures were considered 'agonistic interactions and social grooming was
192 considered an 'affiliative' interaction. When multiple interactions occurred between the same
193 individuals consecutively (e.g. a cow head butts the focal cow three times), interactions were recorded
194 as one event provided the time between each interaction was <10 seconds. Additionally, we recorded
195 the identity of the focal cow's 'nearest neighbour' (or multiple neighbours when there were two or
196 more cows equidistant to the focal) at 2 minute intervals. The nearest neighbour was identified as the
197 cow (any part of body) that was closest to the head of the focal cow; if the closest cow was over 5
198 cow body lengths away from the focal it was not recorded and the focal cow was considered to have
199 no neighbours. We only included dyads in our analyses that had been recorded as nearest neighbours
200 >10 times, indicating a level of opportunity to interact during the behavioural observations. We
201 calculated the (Spearman's rank) correlation coefficient between the association strength measured by
202 the loggers, and the number of aggressive and affiliative events between dyads. To calculate statistical
203 significance we permuted (10,000 imputations) association strengths among dyads, while constraining
204 the identity of the focal individual.

205 *Statistical Analysis*

206 We used R statistical software version 3.1.0 (R Core Team, 2013) to prepare and analyse the
207 proximity logger data. Specifically, we used the packages ‘Matrix’ (Bates & Maechler, 2014), ‘sna’
208 (Butts, 2014), ‘igraph’ (Csardi & Nepusz, 2006), ‘MCMCglmm’ (Hadfield, 2010) and ‘vegan’
209 (Oksanen et al., 2013). Principal Components Analysis (PCA) was completed in SPSS v.19, and
210 weighted degree was calculated using UCINET v.6 (Borgatti, Everett, & Freeman, 1999).

211 Our observed networks were completely saturated (meaning that all possible dyadic
212 interactions occurred in the data). In a binary sense our network data thus has no structural topology,
213 as each cow encountered every other. Because of this we focus much of our analysis of network
214 structure on the edge weights. To reveal social structure at differing edge weights, we use increasing
215 contact thresholds as an alternative to performing a single test on a saturated weighted network. We
216 treat our data as dyadic and use a multilevel mixed-effects model to examine patterns of social
217 assortment.

218 *Generating expected duration matrices*

219 To control for the effect of farm management practices on associations, observed contact durations
220 between dyads were compared to ‘expected’ durations based on whether or not each cow had access
221 to pasture. Expected values were calculated by separately summing the total duration that each cow
222 was in contact with all others *with* and *without* pasture access, then assigning the mean value to each
223 dyad (corresponding to pasture access). This was done for each cow individually to account for the
224 individual differences in total contact time. Therefore each expected matrix estimates the associations
225 between each dyad if cows showed no social preference.

226 *Group-level patterns*

227 *Community structure*

228 We tested for evidence of community structure, i.e. subsets of individuals that are more closely
229 connected to each other than to the rest of the network, using Newman’s modularity clustering
230 algorithm (Newman, 2006a, 2006b). This method finds the most parsimonious partitioning of a

231 network, in which the number and weights of edges are maximised within communities, and
 232 minimised between communities. The ‘best’ partitioning of a network is the one that maximises the
 233 modularity coefficient, Q , resulting in individuals belonging to one or more clusters (Lusseau,
 234 Whitehead, & Gero, 2009). We tested for community structure at increasing contact thresholds as an
 235 alternative to performing a single test on a saturated weighted network. We filtered networks to
 236 contain only associations that were 0-3.25 (in intervals of .25) times the expected value for each dyad,
 237 and then binarised the connections that remained. We compared the maximum modularity value for
 238 each of our filtered observed networks with a suite of values generated by 4999 null networks; each
 239 null network was made by randomising (within individuals) the filtered and binarised networks. We
 240 included the observed maximum Q in the distribution of null networks as it could have arisen by
 241 chance, thus $n=5000$. We used Equation 1 to calculate a p -value (one-tailed).

242 Equation 1:
$$p = \frac{\text{number of } Q(\text{null}) \text{ values} \geq S(\text{obs})}{n}$$

243 *Centralisation*

244 We tested for significant centralisation in the networks, using betweenness centralisation as a test
 245 statistic (Freeman, 1979), and performed this on the observed and 4999 null networks with isolates
 246 removed. Betweenness centralisation is a measure of the individual variation in betweenness
 247 centrality within the network; a star network would be an example of perfect centralisation ($c=1$). We
 248 compared the observed betweenness centralisation of our observed networks with betweenness
 249 centralisation of null networks (as described above for community structure). Again, networks were
 250 tested at increasing filter thresholds (0-3.25 x expected, at .25 intervals).

251 *Network stability*

252 We examined the stability of associations through time at the group level. Each one-month association
 253 matrix was divided into 4 week-long periods, which were compared with each other. To determine the
 254 correlation between two given matrices (with the same actors) we calculated a Spearman’s rank
 255 correlation coefficient. We generated a p -value by comparing the observed coefficient to a distribution

256 of coefficients produced by a null model. Edge-level permutations in the null matrices were stratified
257 according to cows' pasture access; values were permuted between those dyads that had pasture access,
258 dyads that did not have pasture access, and dyads in which one cow had pasture access and the other
259 did not.

260 *Individual-level patterns*

261 *Social differentiation*

262 To assess whether associations between cows were more heterogeneous than we would expect given a
263 null hypothesis that all cows associate uniformly (while accounting for pasture access), we calculated
264 the following statistic for social differentiation using Equation 2 (based on Whitehead (2008);
265 appendix 9.4).

266 Equation 2:
$$S = \frac{\sum_i^N \sum_j^N (O_{ij} - E_{ij})^2}{N(N-1)}$$

267 In this equation the difference between the observed value and the expected value is summed for each
268 dyad, and then divided by the total number of dyads.

269 *Assortment*

270 In order to test for assortment of individuals based on known attributes, we fit mixed-effect models
271 using a Markov Chain Monte Carlo (MCMC) framework. We tested for significant relationships
272 between the dependent variable, association strength, and the following fixed factors: gregariousness,
273 lactation number, pasture access, breed and milk production. To measure milk production, we
274 quantified DIM and milk yield. Because these variables were highly correlated, we used the principal
275 component between the two as a variable. This component accounted for a considerable proportion of
276 the total variance: 82.4%, 80.4%, 78.2%, and 68.1% for deployments 1-4 respectively. We used the
277 weighted degree of each node in a network, which is the sum of the strength of edges connected to
278 each node (Croft et al., 2008) (in this case, the total duration of time each cow spent in proximity to
279 other cows), as a basic measure of individual gregariousness. We calculated the absolute difference in

value between all dyads for each explanatory variable. For example, if cow A was in her 2nd lactation and cow B was in her 5th lactation, the value awarded to that dyad for ‘lactation number’ was 3. Because breed is a categorical variable, we award dyads a ‘0’ if they were of the same breed and a ‘1’ if they were of different breed. Similarly, pasture access was coded as ‘0’ if dyads had the same access and ‘1’ if they did not. We included cow ID as a random effect in all models. The membership modelling capacity of the MCMCglmm package (Hadfield, 2010) accounts for the undirected nature of association measures that result in each cow ID appearing as both individual A and individual B in a dyad. To satisfy assumptions of normality, we log-transformed the dependent variable. As our network is completely saturated, we have made the assumption that transitivity (if *A* and *B* are connected and *B* and *C* are connected, then there is a greater chance of *A* and *C* being connected) in our network is negligible (see Snijders (2011)). Using a Bayesian approach, we ran MCMCglmm models with all possible combinations of fixed factors (gregariousness, lactation number, breed, and pasture access), then identified the best fitting model as the one with the lowest deviance information criterion (DIC) (Spiegelhalter, Best, Carlin, & Van Der Linde, 2002). As milk production determines pasture access, fixed factors could not be included together in the models. We therefore ran additional models to test for assortment by milk production, using a subset of cows that did not have pasture access (as a greater proportion of cows did not have pasture access).

297

298 RESULTS

299

300 *Measuring the relationship between proximity data and social interactions*

301 As two of the focal cows’ loggers malfunctioned during deployment 4, we were only able to include
 302 data from eight of the focal cows in this analysis. There was no relationship between the association
 303 strength recorded by the proximity loggers and the number of aggressive events between cows ($r=$
 304 0.07, $n=63$, $p=0.51$, fig. 1a). In contrast, we found a significant positive relationship between the

305 association strength recorded by loggers and the number of affiliative (grooming) events between
306 cows ($r=0.51$, $n=63$, $p<0.0001$, fig. 1b).

307 *Group-level patterns*

308 *Community structure*

309 There was no evidence of community structure at any contact threshold (fig. 2) in the four deployment
310 networks (fig. 3).

311 *Centralisation*

312 In all four deployments, networks filtered above and including 0.25 times the expected association
313 showed significant centralisation (fig. 4), $p=0.0002$ in all cases (excluding deployment 2 at a threshold
314 of 2.75 times the expected association).

315 *Network stability*

316 All week long association matrices (within a given deployment) were significantly positively
317 correlated (table 2). The effect size of correlations between consecutive matrices ranged from $R^2=$
318 0.176 to $R^2=0.576$.

319 *Individual-level patterns*

320 *Social differentiation*

321 There was significant social differentiation in all four deployment networks (table 3); cows associated
322 with some individuals more and other individuals less, than would be expected by chance ($p < 0.001$
323 for all 4 deployments).

324 *Assortment*

325 For all deployments, the model that best predicted the association strength contained all four
326 variables: gregariousness, lactation number, pasture access and breed (table 4). Across all
327 deployments there was significant positive assortment by lactation number. Significant positive

assortment by breed was found in deployments 1-3. Cows were significantly positively assorted by gregariousness in deployments 1 and 2, and significantly negatively assorted by gregariousness in deployment 3. In deployment 4 there was a trend for negative assortment by gregariousness and positive assortment by breed, but these were not significant. A second model showed there was also positive assortment by milk production for cows without pasture access in all deployments; this pattern was significant for deployments 1 (post. mean= -0.016, $p= 0.026$) and 2 (post. mean= -0.03, $p<0.001$) but not for deployments 3 (post. mean= -0.012, $p= 0.302$) and 4 (post. mean= -0.003, $p= 0.762$).

DISCUSSION

In the current study, we investigated the social network structure of a dynamic group of lactating dairy cows at two social scales. At the group level, we found significant network centralisation and no evidence of community sub-structure. At the individual level, we found evidence for differentiated social relationships and association strength between cows being related to attribute similarity. We tested whether our spatial proximity networks were reflective of social interactions between individuals: an important assumption to validate when using this type of data (Farine, 2015). There was a significant positive correlation between the association strength measured by the proximity loggers, and the number of social grooming events recorded during behavioural observations. This supports the use of this method for measuring social preferences and relationships between cattle, and corresponds to findings of previous studies (Val-Laillet, Guesdon, von Keyserlingk, de Passillé, and Rushen (2009).

The absence of substructure in the current study is consistent with findings by Gygax et al. (2010) who analysed six herds of 24-43 individuals and found that each network was connected as a single component. Stocking density in this study was $9.5\text{m}^2/\text{cow}$ (assuming an average group size of 110 cows and that all cows were inside the barn) which is just over current Red Tractor Assurance guidelines ($10\text{m}^2/\text{cow}$ for a 700-799g cow in a straw bedded system; Red Tractor Farm Assurance Dairy Scheme, 2014). This may have limited the potential for cows to avoid other individuals and for

354 the formation of spatial divisions. In fact, space was further reduced during routine husbandry: cows
355 were restricted to one half of the barn during the distribution of straw bedding (for approximately 45
356 minutes, twice a day) and when bedding areas were scraped out (for approximately 3 hours on every
357 10th day). Maintaining suitable inter-individual distance according to partner preferences and social
358 status reduces conflict between cattle, and thus decreases social stress (Miller & Wood-Gush, 1991;
359 O'Connell, Giller, & Meaney, 1989). Further research into the effects of space allowance on social
360 structure would be particularly beneficial.

361 Significant network centralisation suggests that a few key cows may be particularly
362 influential in terms of social structure, and by consequence these individuals may have
363 disproportionate influence over the rate of disease spread, and the maintenance of group stability.
364 Furthermore, betweenness centralisation can be important for a network's robustness to regrouping
365 (Makagon, McCowan, & Mench, 2012). Assessing social instability and its consequences is crucial to
366 the dairy industry, as group perturbation is known to have negative effects on the welfare and
367 production of cows (Bouissou et al., 2001; Hasegawa et al., 1997; Hultgren & Svensson, 2009; Raussi
368 et al., 2005; von Keyserlingk et al., 2008). At the group level, cows showed some consistency in their
369 social associations. Our results suggest that up to 57% of the social structure in one week is repeated
370 in the following week. However in some cases the amount of repeated structure is as low as 17% for
371 consecutive weeks, indicating a substantial (83%) change in network structure. Though we only
372 analysed a subset of the cows in the milking group (those present for the entirety of a deployment), we
373 remind readers that group composition was dynamic. During deployments, a number of cows that
374 were not included in analyses were moved into and out of the milking group, which likely had some
375 effect on the relationships between cows that were included in the analyses.

376 Correlations indicating network stability for deployment 3 were markedly lower than that of
377 other deployments; this is not easily accounted for by group movements, which were not noticeably
378 different for deployment 3. A potential explanation is that although the number of individuals moved
379 in deployment 3 does not appear particularly conspicuous, the identity of those individuals differed,
380 which may be significant. Individuals occupying certain network positions can have more influence

381 on network structure than others, and so their introduction or removal from a group can have a greater
382 impact (Makagon et al., 2012). ‘Knockout’ experiments on a large, captive group of pigtailed
383 macaques (*Macaca nemestrina*) carried out by Flack et al. (2006) revealed that network structure was
384 largely influenced by a small subset of individuals who performed a specific role in conflict
385 management. These ‘keystone individuals’ (as termed by Pruitt and Keiser (2014)) can be
386 characterised in some animal groups by factors such as dominance (e.g. in lekking species; Robel and
387 Ballard (1974)), status (e.g. in species with a highly developed class system; Aron, Passera, and
388 Keller (1994)) and personality (Pruitt & Keiser, 2014). We encourage further research to investigate
389 this effect in farm animals, including the characteristics and/or roles of individuals that hold positions
390 in the network deemed particularly important for network stability. Conclusions from such studies
391 could be applied in husbandry to increase animal welfare and production.

392 There was significant social differentiation in the relationships between cows; individuals
393 associated more or less with some individuals than would be expected if social associations occurred
394 at random. This supports previous findings that cows interact non-uniformly, often forming
395 preferential relationships with some while avoiding other individuals (Gygax et al., 2010; Reinhardt &
396 Reinhardt, 1981; Wasilewski, 2003). We explored some factors that could account for the non-
397 random associations observed in the networks, testing for network assortment: a measure of the
398 tendency of individuals to associate with others that share their characteristics (Wolf, Mawdsley,
399 Trillmich, & James, 2007). This is commonly observed in human groups, with association due to
400 similar race, ethnicity, age, religion etc. having a huge impact on social preferences (McPherson,
401 Smith-Lovin, & Cook, 2001). The benefits of assortative mixing can be explained by group synchrony
402 because, in order for a group to function efficiently, activities such as foraging, travelling and resting
403 should be coordinated (Conradt & Roper, 2000). Variation in classes such as age, sex or size may
404 result in differences in energy requirements and motivation (e.g. larger individuals may require longer
405 or more frequent foraging bouts than smaller individuals) and deviation from an individual’s optimal
406 activity budget may come at some cost. This may lead to individuals associating more with others that
407 are similar to themselves. Assortativity can lead to group segregation (Conradt & Roper, 2000), as

408 observed in some wild ungulates such as bighorn sheep (*Ovis canadensis*) (Conradt, 1998) and red
409 deer (*Cervus elaphus*) (Ruckstuhl & Neuhaus, 2002) who spend most of their lives in all-male or all-
410 female groups that only re-join periodically, such as during the breeding season. There is also
411 evidence of assortment by kin in some animal societies (Silk, Altmann, & Alberts, 2006; Ward &
412 Hart, 2003; Wiszniewski, Lusseau, & Möller, 2010).

413 The influence of assortment on network structure has been investigated in previous studies
414 (e.g. trinidadian guppies (Croft et al., 2005); pigtailed macaques (Flack et al., 2006); bottlenose
415 dolphins (Lusseau & Newman, 2004)) but this study is the first (to the authors' knowledge) to
416 investigate these patterns in a farm animal species. Behavioural synchrony has been observed in
417 cattle, and synchronised lying has been used as a welfare indicator (Fregonesi & Leaver, 2001). Stoye,
418 Porter, and Stamp Dawkins (2012) found that cows were more synchronised with their nearest
419 neighbours (than other randomly selected individuals in the group) and suggest that postural
420 synchronisation in cattle is the result of both social facilitation and concurrent activity cycles. In this
421 study, we found significant patterns of assortative mixing by breed, milk production, pasture access,
422 lactation number and gregariousness. Cows associated more with those of the same breed to
423 themselves (significant for deployments 1-3). The different breeds in the study group may be
424 reflective of body mass and energy requirements (and by extension, activity budget). For example,
425 most Holstein-Friesian cows were notably larger than most Ayrshire cows. Cows associated more with
426 those similar in milk production in all deployments, and these patterns were statistically significant for
427 deployments 1 and 2. Assortative mixing by milk production may also be related to energy
428 requirements, which vary with stage of lactation/pregnancy and yield (Coulon & Rémond, 1991).
429 Additionally, DIM is a measure of how long a cow has been present in the milking group and thus is a
430 measure of the opportunity for social contact and bond formation. Cows associated significantly more
431 with others of similar lactation number. This measure reflects age, which may affect energy demands
432 to some extent, but is likely to be more significant in terms of familiarity between individuals; the
433 amount of previous experience of conspecifics may be directly related to strength of bonds. Indeed,
434 familiarity has been identified as an important factor for social relationships in previous studies

435 (Gygax et al., 2010; Takeda, Sato, & Sugawara, 2003; Wikberg, Ting, & Sicotte, 2014). In a study by
436 Gygax et al. (2010), synchronicity was significantly affected by whether or not cows were reared
437 together and/or had been together during the latest dry period.

438 Individuals were significantly assorted by gregariousness in all four networks. However the
439 direction of the effect differed, highlighting the advantage of repeated data periods in this study. In
440 deployments 1 and 2 cows associated significantly more with those with similar gregariousness values
441 to themselves, while in deployments 3 and 4 cows associated less with others of similar
442 gregariousness (this pattern was significant in deployment 3). Further work is required to determine
443 which factors drive temporal dynamics in the social networks of dairy cattle. Assortment by
444 gregariousness has been reported in other species (Croft et al., 2005; Lusseau et al., 2006) . It infers
445 association with others of access to similar social resources (Flack et al., 2006) and may have
446 implications for the spread of disease and information (Croft et al., 2005). Although significant
447 assortment was found in the networks, these relationships were surprisingly weak; the variables we
448 tested accounted for only a small amount of variation in the observed association patterns. In addition
449 to the removal of cows for culling or selling, cows in this herd calve all year round, resulting in
450 regular change in the milking group's composition. The relationships that form may be dynamic, with
451 more temporary bonds forming due to factors not accounted for here. The dominance hierarchy is
452 likely to influence mixing patterns, as it determines individuals' access to resources, which could have
453 implications for space use and proximity to others. For example, when resources such as lying areas
454 are limited and of unequal quality, more dominant individuals will gain access to more favourable
455 positions, perhaps resulting in these cows lying in closer proximity. At the study farm, cows
456 voluntarily enter a waiting area when they are due to be milked, and then compete for entry to one of
457 two milking units. As cows cannot leave the waiting area until they have been milked, the time spent
458 in this small space is largely determined by dominance, therefore prolonged proximity between
459 subordinates may be inevitable in some cases. As such, mixing patterns can help identify problems in
460 farm animal groups, such as when high avoidance patterns lead to uneven distribution of resources
461 (Koene & Ipema, 2014)

462

463 *Conclusions*

464 Fundamental to investigations into the social components of welfare and productivity, is a thorough
465 understanding of the structure in which social mechanisms occur. Our results shed light on the factors
466 affecting the social network structure of dairy cows in a commercial farm setting. Networks did not
467 indicate any community structure; however we found significant centralisation in all deployment
468 periods. Relationships between individuals were differentiated, with cows associating non-randomly,
469 and there was assortative mixing based on lactation number, breed, gregariousness and milk
470 production. Analyses revealed relatively low network stability which may have implications for
471 welfare and productivity via social stress. This study demonstrates the use of innovative automated
472 tools and social network analysis for understanding social relationships in farm animal groups, both of
473 which are likely to play an important role in the future of animal welfare science.

474

475 ETHICAL STATEMENT

476 This study was non-invasive and the data collection protocol was approved by the School of
477 Psychology's Ethical Review Group at the University of Exeter. Deployment of collars was
478 coordinated with routine management practice when possible, to minimise any stress associated with
479 handling.

480

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488

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650

651 FIGURE CAPTIONS

652 Figure 1. Correlation between the association strength recorded by the proximity loggers and the
653 number of (a) aggressive ($r=0.07$, $n=63$, $p=0.51$) and (b) affiliative ($r=0.51$, $n=63$, $p<0.0001$) events
654 observed between cows during behavioural observations (p-values are based on permutation tests)

655

656 Figure 2. Patterns of community structure during the four logger deployments. There was no
657 significant community structure found at any filter threshold for deployments 1-4 (a-d). Empty circles
658 indicate the observed maximum modularity for each network. Solid circles indicate the maximum
659 modularity generated by the null model, with arrows specifying 95% confidence intervals

660

661 Figure 3. Visualisation of cow social networks that have been filtered to only include total
662 associations that were 2 (a), 2.5 (b) or 3 (c) times longer than expected based on networks generated
663 by a null model (controlling for pasture access), for deployments 1-4

664

665 Figure 4. Network betweenness centralisation at increasing filter thresholds for deployments 1-4 (a-d).
666 Empty circles indicate the observed mean betweenness centralisation in each network. Solid circles
667 indicate the mean betweenness centralisation generated by the null model, with arrows specifying

668 95% confidence intervals. Filtered networks showed significant betweenness centralisation, except for
669 deployment 2 at a threshold of 2.75 ($p=0.1$)
670

Table 1. Descriptive statistics of cows included in analyses and others in the milking group during each deployment

Deployment		1	2	3	4
Data period		08/11/12 to 06/12/12	22/12/12 to 18/01/13	14/03/13 to 09/04/13	13/05/13 to 09/06/13
Cows included in analyses	N	94	73	59	64
	<i>Breed:</i>				
	Ayrshire	20	11	7	8
	British Friesian	3	3	3	3
	Brown Swiss Cross	2	4	3	3
	Holstein Friesian	44	37	34	37
	Holstein Friesian Cross	6	6	2	4
	Holstein	16	10	9	6
	Holstein Cross	1	1	1	1
	British Shorthorn	0	1	1	1
	Pasture access - Y	59	69	45	48
	Pasture access - N	35	4	28	16
All cows in milking group	Total N	125	114	114	117
	N calved	9	6	8	4
	N dried off	9	5	3	6
	N given pasture access within deployment	2	1	6	6

Table 2. Spearman's rank correlations between each week-long matrix, measuring network stability for deployments 1-4. Significance was calculated using a null model with edge-level permutations, stratified according to cows' pasture access

Week-long matrices	Deployment			
	1	2	3	4
1 and 2	$R^2=.421^*$	$R^2=.415^*$	$R^2=.26^*$	$R^2=.501^*$
2 and 3	$R^2=.424^*$	$R^2=.368^*$	$R^2=.198^*$	$R^2=.524^*$
3 and 4	$R^2=.462^*$	$R^2=.327^*$	$R^2=.176^*$	$R^2=.576^*$
1 and 3	$R^2=.378^*$	$R^2=.332^*$	$R^2=.173^*$	$R^2=.433^*$
2 and 4	$R^2=.378^*$	$R^2=.401^*$	$R^2=.112^*$	$R^2=.482^*$
1 and 4	$R^2=.377^*$	$R^2=.371^*$	$R^2=.034^{**}$	$R^2=.416^*$
* $p=.0002$, ** $p=.031$				

Table 3. The social differentiation measured in deployments 1-4, indicates that cows were significantly more heterogeneous than we would expect given a null hypothesis that all cows associate uniformly (while accounting for pasture access)

Deployment	Social differentiation		95% quantile	p value
	Observed	Median of Nulls	of null distribution	
1	30274488	998195.5	1027177	0.0002
2	29276011	965649.8	999924.9	0.0002
3	31105959	1100702	1148958	0.0002
4	39014159	953668.4	995659.7	0.0002

Table 4. Results of best fitting model (indicated by lowest deviance information criterion) from mixed model regression, measuring assortment of cows by traits in deployments 1-4

Deployment	Factor	Posterior mean	l-95% CI	u-95% CI	<i>p</i>
1	(Intercept)	3.996	3.938	4.065	<0.001
	Degree	-0.0004	-0.0007	-0.0002	<0.001
	Lactation number	-0.019	-0.024	-0.015	<0.001
	Pasture access	-0.13	-0.142	-0.117	<0.001
	Breed	-0.048	-0.034	-0.061	<0.001
2	(Intercept)	3.969	3.912	4.037	<.001
	Degree	-0.0006	-0.001	-0.0002	0.002
	Lactation number	-0.021	-0.026	-0.016	<0.001
	Pasture access	-0.087	-0.146	-0.022	0.004
	Breed	-0.031	-0.011	-0.049	-0.002
3	(Intercept)	4.031	3.965	4.09	<0.001
	Degree	0.0013	0.009	0.0019	<0.001
	Lactation number	-0.014	-0.019	-0.008	<0.001
	Pasture access	-0.013	-0.027	0.004	0.098
	Breed	-0.024	-0.004	-0.048	0.036
4	(Intercept)	3.925	3.834	4.02	<0.001
	Degree	0.0004	0.0001	0.0008	0.094
	Lactation number	-0.018	-0.023	-0.013	<0.001
	Pasture access	-0.287	-0.308	-0.267	<0.001
	Breed	-0.022	-0.002	-0.048	0.11

Figure

Figure 1

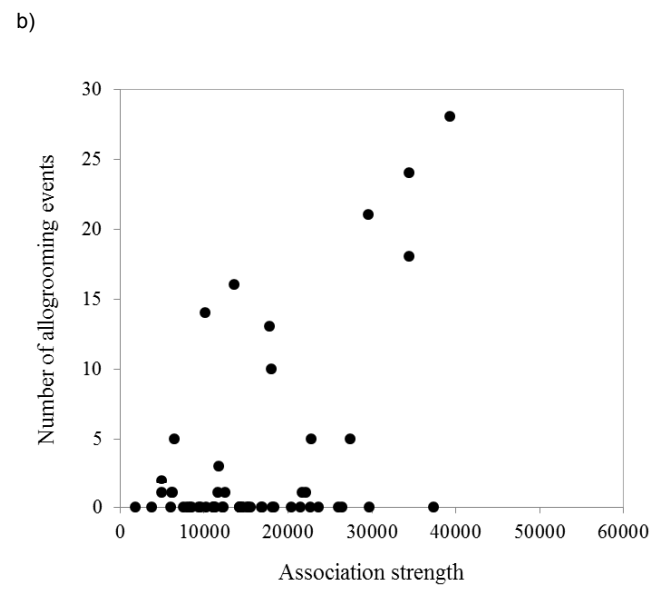
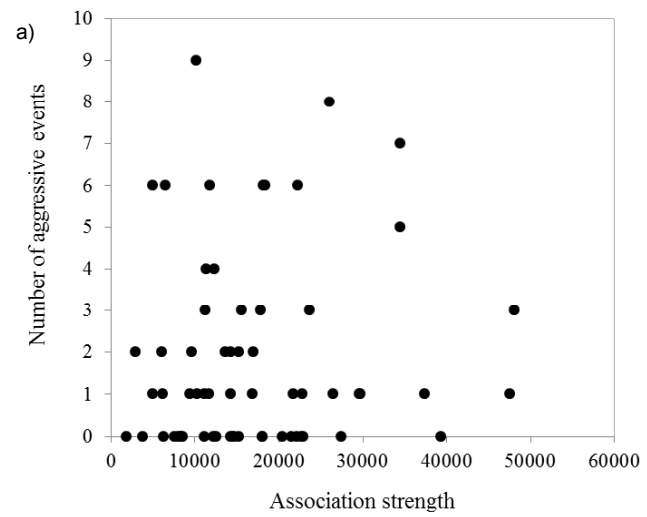


Figure 2

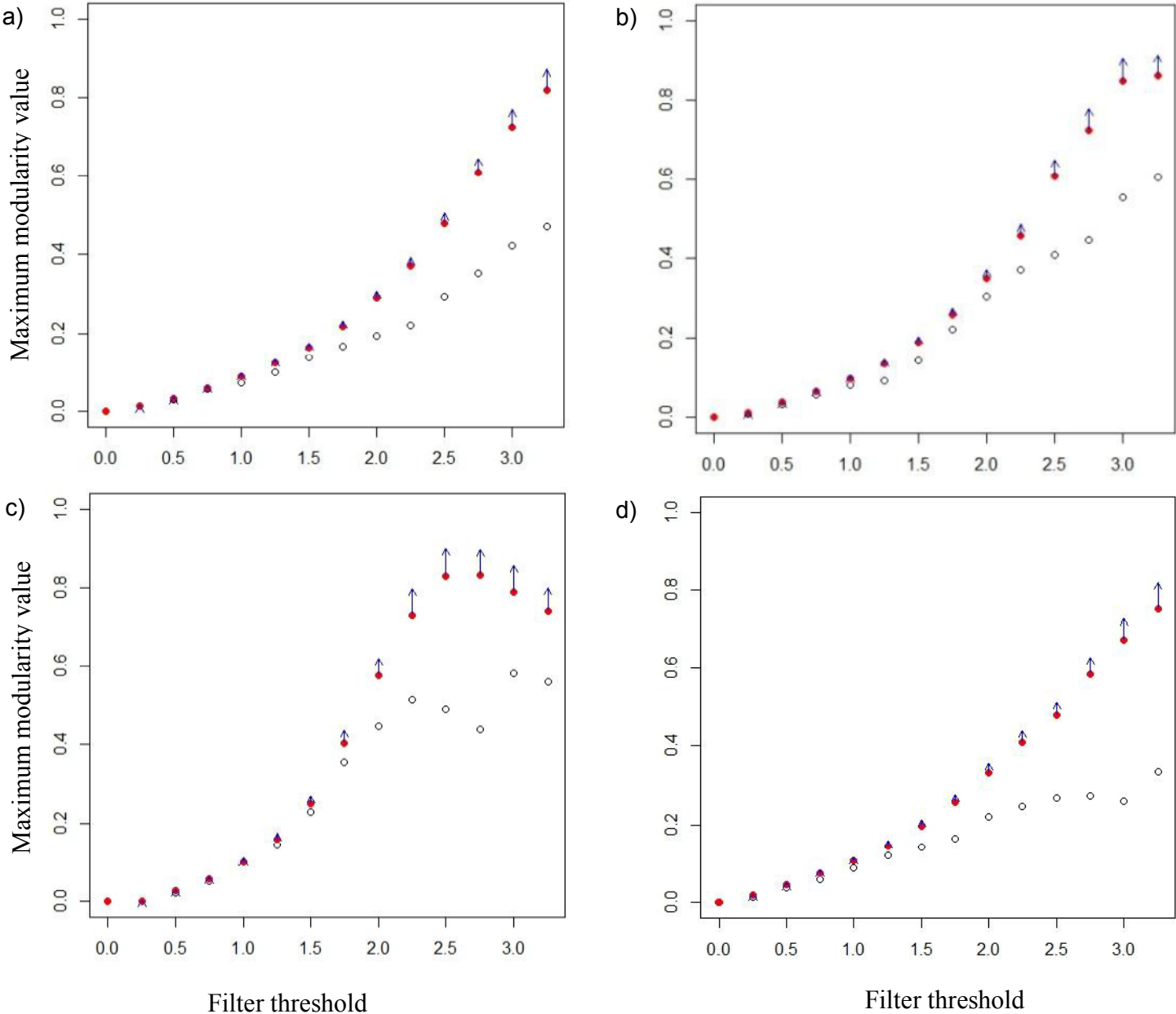


Figure 3

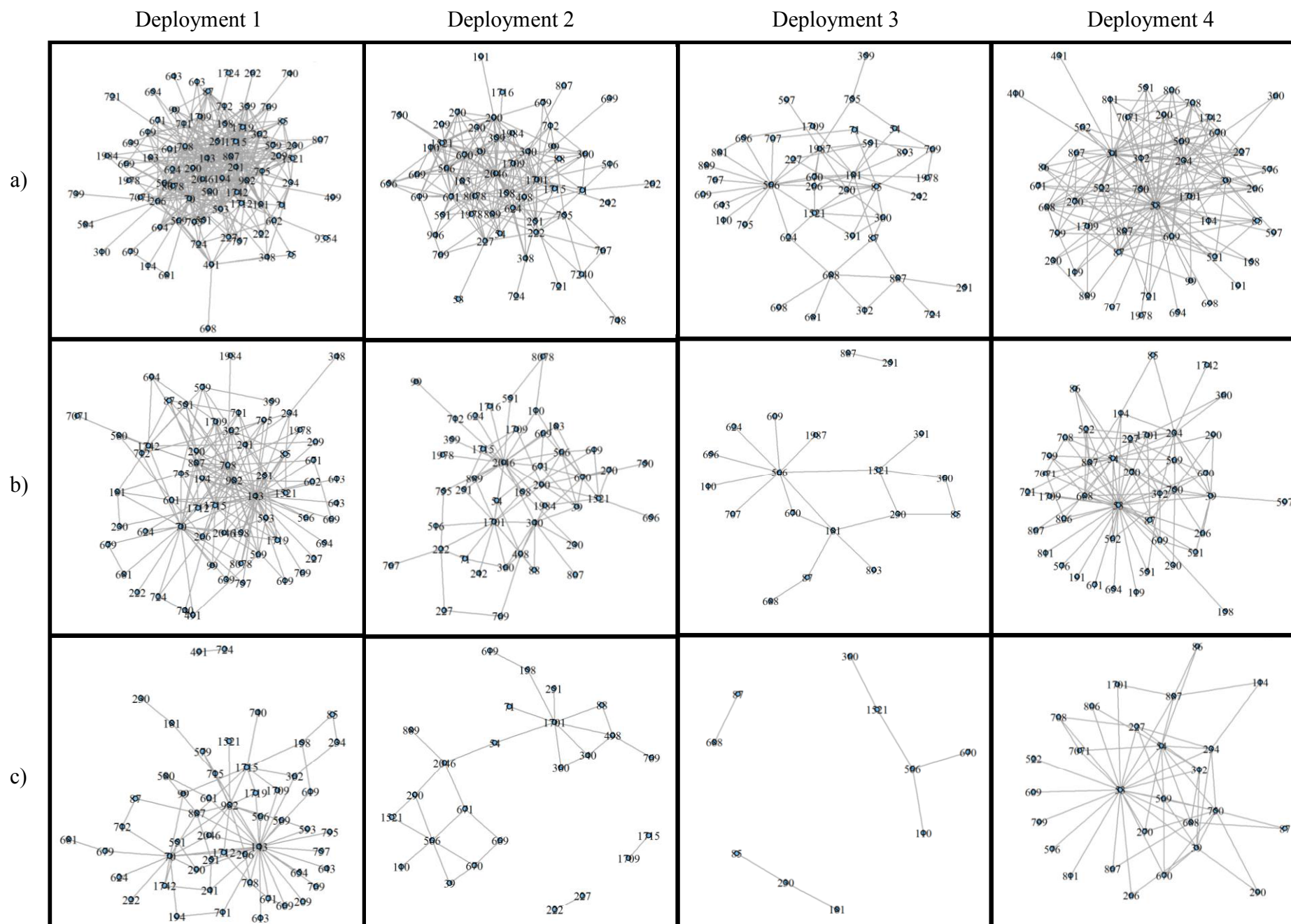


Figure 4

